EVALUATION OF GENE BREED TYPE AND EXPRESSION OF FEED EFFICIENCY CANDIDATE GENES, AND THEIR ASSOCIATIONS WITH CARCASS TRAITS IN F_2 NELLORE-ANGUS STEERS

A Thesis

by

JESSICA MARIE CARDIN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2011

Major Subject: Animal Breeding

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Co-Chairs of Committee:	Andy D. Herring
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ABSTRACT

Evaluation of Gene Breed Type and Expression of Feed Efficiency Candidate Genes, and Their Associations With Carcass Traits in F_2 Nellore-Angus Steers. (August 2011)

Jessica Marie Cardin, B.S., California State University, Chico

Co-Chairs of Advisory Committee: Dr. Andy D. Herring
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Steers produced in Cycle I of the Texas A&M University McGregor Genomics Project (n = 232, F_2 Nellore-Angus) were evaluated for carcass composition, visceral organ weights, and model predicted residual consumption (MPRC), a measure of feed efficiency. Hot carcass weight was strongly correlated with liver weight (r = 0.70, $P < 0.001$) heart weight (r = 0.58, $P < 0.001$), and viscera weight (r = 0.55, $P < 0.001$) but not spleen weight (r = -0.01, $P = 0.83$). Liver, heart and viscera weights were moderately positively correlated with external and kidney pelvic heart fat (KPH), but not with marbling. None of the organ weights were correlated with MPRC.

A subset of 54 animals was selected for extreme values of residuals of MPRC after a mixed model analysis that included fixed effects of sire and family nested within sire, and these animals were evaluated for insulin-like growth factor I (*IGFI)* expression in liver samples collected at harvest through quantitative real time polymerase chain reaction (qRT-PCR). *IGFI* relative quantity (*IGFI* RQ) was collected from qRT-PCR and was correlated with liver (r = -0.23, $P = 0.09$), spleen (r = 0.48, $P <0.001$) and viscera weight (r = 0.24, $P = 0.08$), but not any carcass trait or MPRC residual.

Gene breed types were determined for 4 candidate genes of feed efficiency: insulin like growth factor-1 (*IGF1*), leptin (*LEP*), neuropeptide-Y (*NPY*) and ghrelin (*GHRL*). Gene breed types were represented as AA, AN, NA, and NN where A and N denote Angus and Nellore, respectively, and paternal inheritance is listed first. Given that contemporary group significantly influenced most traits (MPRC, all carcass traits, liver weight and viscera weight), effects of gene breed type and contemporary group were evaluated together in analyses. *GHRL* influenced liver ($P = 0.02$) and viscera weight ($P = 0.02$), *IGF1* influenced kidney, pelvic, and heart fat ($P = 0.05$), *NPY* influenced liver weight ($P = 0.03$) and hot carcass weight ($P = 0.04$), and *LEP* influenced ribeye area ($P = 0.05$) and hot carcass weight ($P = 0.04$) with a tendency to influence liver weight ($P = 0.06$).

Alternate heterozygotes for *GHRL* were statistically different in liver weight and viscera weight where NA was heavier than AN. Alternate heterozygotes for *LEP* did not differ in ribeye area, hot carcass weight, or liver weight. Alternate heterozygotes for *NPY* differed in liver weight (NA heavier than AN), but did not differ in hot carcass weight. Carcasses with AA for *LEP* and *NPY* were 18 to 19 kg heavier ($P < 0.05$) than those with NN, with heterozygotes intermediate.

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1. INTRODUCTION

Improved feed efficiency, which reduces the amount of feed needed by each animal, while still achieving the same level of performance, could have large impacts on different stages of the beef industry. Cow-calf producers, stocker operators, and feed yards would be able to reduce operating costs because feed accounts for 60% of production expenses (Pond et al., 1995). Several studies have documented heritability estimates for various measures of feed efficiency that would be of sufficient magnitude for selection. However, implementing significant change in feed efficiency of cattle has been challenging due to questions as to which feed efficiency measurement is best, the associated costs of implementation, and the means to identify animals for use in breeding decisions. Measurements of feed efficiency have also been reported to have undesirable correlations to other production traits. Most previously published efficiency research has also focused on *Bos taurus* cattle, with few studies examining *Bos indicus* cattle or *Bos indicus-Bos taurus* crosses.

Hormones physiologically regulate energy metabolism and appetite stimulation. Leptin (LEP) satiates the appetite and disrupts neuropeptide Y (NPY) production. Ghrelin (GHRL) stimulates the appetite and increases the use of carbohydrates. Neuropeptide Y also induces hunger. Insulin-like growth factor I (IGF1) regulates cell growth and glucose metabolism. Consequently, these hormones and the genes that encode them have received attention as candidates for feed efficiency research.

This thesis follows the style of Journal of Animal Science.

Organ size is another area of research that could provide a better understanding to the biological causes of variation in feed efficiency. Whereas organ weights comprise only 4 to 6% of body mass, they utilize almost half the total amount of ATP produced by the body (Kelly and McBride, 1990; Caton et al., 2000). Few significant correlations have been found between residual feed intake (RFI) and organ weights. However, these studies have been conducted on cattle with genetic backgrounds that are primarily *Bos taurus.* By evaluating cattle with *Bos indicus* influence, this might provide new insight into relationships between organ weights and feed efficiency, given the evolutionary divergence of these two types of cattle.

As a result, the objectives of this project were to: (1) investigate gene breed types for *IGF1*, *LEP*, *NPY*, and *GHRL* for their influence on feed efficiency (model predicted residual consumption; MPRC), visceral organ weights and carcass traits, (2) investigate the gene expression of *IGF1* and *LEP* in liver samples from 54 animals previously identified to be divergent in feed efficiency (based on MPRC residual values) and investigate potential relationships of gene expression with visceral organ weight and carcass traits in these animals, and (3) evaluate correlations of MPRC, organ weights and carcass traits in F_2 *Bos indicus-Bos taurus* steers produced in Cycle I of the McGregor Genomics Project.

2. LITERATURE REVIEW

2.1 Measures of Feed Efficiency

Animal production is the science and art of ultimately converting plant materials into high quality protein, additional animals, and other animal products. Feedstuffs have been reported to account for 60 to 65% of the total feed costs of any beef cattle operation (Pond et al., 1995). Miller et al. (2001) reported that half of herd-to-herd divergence in profitability between beef cow-calf operations could be attributed to feed costs. McWhir and Wilton (1987) found that the efficiency of feed conversion could account for 50% of the variation in the margin of profitability in beef cattle. With rising costs of feed and shrinking profit margins, producers may choose to measure and improve feed efficiency as a means to increase profitability.

Feed efficiency can be measured by several different methods (Archer et al., 1999). A widely used industry method is feed conversion ratio (FCR; kg input per kg output or the inverse). However, FCR is negatively correlated with mature size (Koots et al., 1994; Archer et al., 1999), especially when evaluated at an age-constant or time-constant basis. Thus, selection for improved FCR could lead to increases in cow mature size.

Another method for measuring feed efficiency is RFI first proposed by Koch et al. (1963), which is the difference between predicted intake and actual intake, when accounting for average daily gain (ADG) and body weight (BW). Others have included body composition in the linear regression equation in addition to ADG and BW (Basarab

et al., 2003; Ahola et al., 2007). As large scale individual data collection has become economically feasible due to advances in feeding technology, RFI has received greater attention and has been proposed as the preferred feed efficiency measure by many due to its reported favorable or negligible phenotypic and genetic relationships with feed intake, ADG, FCR, and body weight (Jensen et al., 1992; Arthur et al, 2001a,b; Hoque et al., 2006; Tedeschi et al., 2006; Ahola et al., 2007). Furthermore, improvement in RFI has been reported to be favorably related to methane production, adding an advantageous environmental component to beef cattle selection for feed efficiency (Nkrumah et al., 2006).

Taylor and Field (1999) stated that if beef cattle producers improved feed efficiency by 5%, the result would be equal to: (1) increasing ADG by 0.27 kilograms per day, (2) reducing feed cost by $8 per 0.907 metric ton (per U.S. ton), (3) decreasing the purchase cost of feeder calves by $1.75 per 45.4 kg (per 100 lb), and (4) decreasing interest rate on capital from 15% to 9.5%. However, these types of statements typically oversimplify relationships among supply and demand variables. One of the reasons that producers have not made large improvements in feed efficiency is that it is extremely difficult and costly to measure individual feed intake due to high costs of equipment and labor. Producers have focused primarily on output traits that are simple and inexpensive to measure and have associated value such as weight, size and growth measurements. Most commercial cow-calf producers sell calves close to weaning time so weaning weight drives income in most operations. Fox et al. (2001) used a computer prediction model developed by Tedeschi et al. (2001) called the Cornell Value Discovery System to

simulate the impact of growth rate and feed efficiency on producer costs and profitability. The results indicated an improvement in gain by 10% could increase profit by 18%, but that a 10% increase in feed efficiency could increase profit by 43%.

A difficulty with improving RFI is having a method of selection that will provide consistent results. Cardin et al. (2008) reported that there was no correlation between expected progeny difference (EPD) profiles (birth weight, weaning weight, yearling weight, and milk) and RFI ranking in Angus yearling bulls. Whereas this result may seem discouraging at first, it means that cattle from different body types, genetic potential, and growth potential can have a low RFI ranking. Again, it also means that producers will not be able to look at commonly used EPD to discern the RFI ranking for each bull. Researchers will have to continue to investigate the physiology of cattle to help identify the source of variation for RFI.

Residual feed intake has been found to be moderately heritable which implies that it is a good candidate for genetic improvement (Koch et al., 1963; Arthur et al., 2001a; Crews 2005). Residual feed intake has a reported heritability ranging from 0.28 to 0.58 (Koch et al., 1963; Crews et al., 2003). Across and within different populations of cattle, a large amount of genetic variation for RFI exists (Basarab et al., 2003, Archer and Bergh, 2000; Herd and Bishop, 2000), indicating that selection for RFI is possible and the reduced intake can be obtained in future generations.

Whereas the costs of measuring RFI are prohibitive for many operations, the prospect of using predictive genetic markers is of great interest to many producers. Sherman et al. (2010) conducted a whole genome single nucleotide polymorphism

(SNP) association study using 2633 SNP across 29 autosomes in 464 steers sired by Angus, Charolais, and Alberta Hybrid bulls. There were 150 SNP with allele substitution effects significant at $P < 0.05$ level of which 23 SNP were significant at $P < 0.01$ level. After accounting for multiple testing, none of the SNP reached significance at the $P < 0.05$ level. However, Sherman et al. (2010) urge caution in interpretation of adjusted *P*-values because empirical estimates of the false discovery rate assume the SNP effects are independent. Instead, Sherman et al. (2010) removed 9 SNP from the set of 150 SNP that were strongly associated ($r^2 > 0.8$) and then used both backwards elimination from a multivariate model and calculation of sequential molecular breeding values (MBV) as two alternate approaches to identify a maximally informative panel of SNP. There were 32 SNP included in the multivariate model and 79 SNP retained in the MBV with 27 SNP in common between the approaches. To compare the approaches MBV were also calculated for the 32 SNP and regression of RFI on MBV gave $r^2 = 0.416$ with 32 SNP and $r^2 = 0.497$ with 79 SNP. Spearman correlations were 0.622 and 0.670, respectively. Sherman et al. (2010) concluded that the 79 SNP model was the best model and explained 37.3% of the phenotypic variation in RFI.

Currently, two companies sell genetic tests related to RFI. IGENITY has developed a tool to analyze the genetic makeup of both *Bos indicus* and *Bos taurus* cattle. IGENITY has included RFI and ADG in their analyses. Third party testing found that in a population of 1270 *Bos indicus* influenced cattle the feed efficiency MBV were significantly correlated with RFI (Cornell, 2010). Pfizer Animal Genetics has also entered the market with a test called the GENESTAR® Feed Efficiency MVP that is

based on a 56-marker panel. In a population of 671 *Bos taurus* influenced cattle the GENESTAR® Feed Efficiency MVP was found to have a statistically significant relationship with RFI (Cornell, 2010). However, this same test was found to have no significant relationship with RFI in another population of 395 *Bos indicus* cattle.

Another drawback to RFI is that it is not clear how this measurement can be used across animals of different contemporary groups. Because the regression equation that is used to calculate RFI is derived from each individual group of animals, RFI rankings are unique to each set of animals because the mean RFI value is forced to be zero in each contemporary group. To address this limitation of RFI, an alternate measure of feed efficiency referred to as model predicted residual consumption (MPRC) was calculated based on the NRC (2000) beef cattle model by Amen (2007). The NRC (2000) beef cattle model predicts daily feed intake based on observed weight gain of each individual and standardized inputs for animal type, age, sex, condition, and breed. Thus, MPRC is defined as the difference between the model predicted intake (MDMI) and observed dry matter intake (DMI) (Amen, 2007). As with RFI, if an animal has negative MPRC that animal is considered more efficient because it ate less feed than was predicted from the model; however, the average MPRC is not forced to be zero for a group of animals as with RFI, potentially making it a more useful tool for analysis across multiple contemporary groups of cattle.

2.2 Breed Effects

Breed differences among cattle are long recognized, and crossbreeding of cattle has been practiced for many years. Crossbreeding has been an important method

employed by cow-calf producers to create genetic improvement in their cow herds. To achieve genetic improvement, the crossbreeding system must optimize nonadditive (heterosis) and additive (breed differences) effects of genes (Gregory and Cundiff, 1980; Cundiff, 1970). Crossbreeding can also be used to help cattle adapt to certain climates and to better fit resources (Long, 1980). Another benefit of crossbreeding is that it may provide for complementarity from use of specialized sire and dam types (Cartwright, 1980). It is widely recognized that *Bos taurus-Bos indicus* crosses show high levels of heterosis and productivity. As this research project evaluated crossbred Angus-Nellore steers, a brief discussion of these breeds are provided and research pertaining to feed efficiency in *Bos indicus* influenced cattle is discussed.

Angus cattle originated from Angus and Aberdeen counties in Scotland. They are black, naturally polled cattle that historically have been moderate in size. They are noted to have early compositional and sexual maturity and high intramuscular fat. The females tend to be good mothers and have acceptable milk production. The first Angus cattle were brought into the United States by George Grant, who imported four bulls from Scotland to Kansas in 1873. In the 5 years from 1878 to 1883, more than 1,200 Angus cattle were imported into the United States (Oklahoma State University, 1995). Today, the Angus breed has the greatest number of annual registrations in the U.S. among beef cattle (NPLC, 2010).

The Nellore is a *Bos indicus* cattle breed developed in India. This breed has a distinctive hump over the shoulder that is not found in *Bos taurus* cattle, but is common to *Bos indicus* breeds. Nellore cattle are gray with dark skin and have short horns that

are usually upward projecting. They are noted for their maternal instincts. The breed is also known for being heat and insect tolerant. The increased heat tolerance is due to an increase in size and number of sweat glands. The hide of these animals is thick which prevent penetration by biting insects. The Nellore breed is also very hardy and can perform in adverse nutritional and climatic conditions (Oklahoma State University, 1995). Nellore is one of the foundation Zebu breeds of American Brahman cattle, and current Nellore cattle were brought to the U.S. from Brazil (Sanders, 1980).

Comerford et al. (1991) published results from a diallele study involving Simmental, Limousin, Polled Hereford, and Brahman cattle. In this study it was noted that steers with Brahman sires ate less than steers with Simmental, Limousin or Polled Hereford sires. However, Brahman-sired calves were the least efficient in feed conversion ratio (FCR). Conversely, calves from Brahman and Hereford dams were more efficient than those from Simmental and Limousin dams. Calves from Simmental dams had higher final feedlot weights than calves from Brahman dams. Calves from Polled Hereford sires and Simmental dams and purebred Limousin calves were lighter than the other calves, which allowed them to be more efficient as they had less weight to maintain. The weaning weights were measured at the mean age of 217 days (Comerford, 1988b). When assessing the *Bos taurus* and *Bos indicus* crosses, reciprocal differences were found. Calves out of Hereford dams by Brahman sires were more efficient with an FCR of 6.60 than calves from the reciprocal mating (7.07). In Simmental x Brahman and Limousin x Brahman matings, the opposite was true. The Simmental-sired calves had an FCR of 7.08 versus an FCR of 8.10 for calves with

Simmental dams. The Limousin x Brahman calves followed this same trend and had an FCR of 7.22 whereas Brahman-sired calves had a FCR of 7.74.

Rogerson et al. (1968) used 10 *Bos indicus* Boran-type and 11 *Bos taurus* Hereford-type steers to study the differences of live weight gain. These animals were weaned at 36 weeks and placed into individual stalls that were covered. The animals were fed cubed concentrate ration and lucerne hay. The concentrate ration was comprised of maize, bran, groundnut cake, and molasses. Live animal weights were recorded weekly. The Hereford cattle had higher DMI than the Boran steers. As both types of cattle gained weight, the DMI of Boran cattle dropped in comparison to the *Bos taurus* cattle. It should also be noted that the Boran cattle gained much less than the Hereford cattle. Hereford steers had a daily live-weight gain of 0.9 kg/d whereas the Boran steers had a live-weight gain of 0.45 kg/d. Whereas the Hereford steers ate more feed than the Boran steers, the Herefords were more efficient in terms of FCR because the Herefords gained more weight in a shorter amount of time than the Boran steers.

Frisch and Vercoe (1969) measured weight gain, feed intake and eating rate in Brahman, Africander, and Shorthorn x Hereford cattle using 9 cattle per breed type and 3 of each breed type for each year of study (1966, 1967, 1968). The individuals of each breed type had differing breed compositions. The Brahmans were either 15/16 or purebred and were also highly related. This could have an effect on the study as the animals might not have been an accurate representation of the breed if they were all closely related. The Africanders had more variation in percentage of Africander breed because some animals were 7/8 Africander and others were 3/4 Africander. The

Africander animals were also closely related. As found in previous studies conducted by and alluded to by these authors, the Brahman cattle consumed less feed than the other cattle breeds, and the authors attributed the lower feed intake to lower maintenance requirements for the Brahman breed. At the start of the trial Brahmans also weighed more (307.3 kg) than the other breeds (S x H 264.3 kg and Africander 270.7 kg), which Frisch and Vercoe (1969) attributed to differences in grazing conditions until the cattle were placed on the study.

Robinson and Oddy (2004) conducted a study with 524 steers and 172 heifers that were from tropically adapted Brahman, Belmont Red and Santa Gertrudis herds. The study also included 785 steers that were from temperate Angus, Hereford, Murray Grey, and Shorthorn herds. These cattle were fed out to meet 3 different markets; Australian, Korean and Japanese. The Australian market target weight was 400 kg, Korean target weight was 520 kg, and the Japanese market weight was 600 kg. The mean weight gain of steers from the temperate breeds was 1.73 ± 0.26 kg/d whereas the mean weight gain of steers from tropically adapted breeds was 1.58 ± 0.33 kg/d. The steers from the temperate breeds also ate fewer times (7.9 ± 2.6) per d with longer time spent eating (105 ± 20 min/d) than the tropically adapted steers who ate 15.9 ± 5.2 times per d and spent 96 ± 26 min/d eating. There was also a low phenotypic correlation (r = 0.16) and genotypic correlation (r = 0.18) between RFI and number of eating sessions. This suggests that efficient animals make fewer trips to the feed bunk.

2.3 Feed Efficiency Candidate Genes

To better understand the biological cause of variation between individuals, scientists will need to investigate the signals that regulate food intake and energy homeostasis. Energy homeostasis is achieved when the anabolic and catabolic activities of the body are in balance over a long period of time (Woods et al., 1998). Leptin is secreted by adipose tissue and in response to the status of energy balance of the body. Ghrelin is secreted by the stomach and regulates feeding behavior in the short term and regulates energy metabolism in the long term (Meier, et al., 2004). Adiponectin decreases insulin resistance and blood glucose concentrations (Meier et al., 2004). Neuropeptide Y is a neurotransmitter that has a well-defined pathway in the hypothalamus that regulates the energy homeostasis of individuals. Insulin-like growth factor 1 plays a role in childhood growth and continues to have anabolic effects in adults. Once IGF1 is bound to its receptor, activation of the phosphoinositide-3-kinase (PI3K) and murine thymoma viral oncogene homolog (AKT1) signaling pathways stimulates cell growth (Gerrard and Grant, 2007). These signal peptides not only affect the energy metabolism of the individual, but can also regulate glucose metabolism with subsequent effects on other organ systems including liver, brain, and skeletal muscle.

2.3a Adiponectin

Adiponectin (ADIPOQ) is a 30 kDa protein that is also known as adipocyte complement related protein (Meier et al., 2004). Adiponectin plays a role in glucose and lipid homeostasis by increasing fatty acid oxidation and decreasing fat deposition and is secreted exclusively from adipose tissue. Levels of this hormone are inversely related to

body fat percentage in adult humans (Ukkola et al., 2002). Adiponectin concentration is an example of sexual dimorphism as females have higher circulating levels than males. Differing levels of expression can also be found in diabetics when compared to non-diabetics (Nedvídková et al., 2005). Morsci et al. (2006) found that in Angus cattle no SNP were associated with marbling when an additive model was used, in comparison to the general model, but they also found associations between 3 adiponectin SNP and fat thickness and rib eye area. The most significant relationship was found for *ADIPOQ*:g.1596G>A, a position in the promoter region that could affect the rate of transcription of *ADIPOQ*. However, *ADIPOQ*:g.1436-1506dup is under stronger selection so the SNP in the promoter is probably not causal (Morsci et al, 2006).

2.3b Leptin

The role of leptin in the body is to regulate whole-body energy metabolism, which makes it a prime physiological marker for food intake, body weight, and energy expenditure (Houseknecht et al., 1998; Woods et al., 1998). Leptin decreases neuropeptide Y (NPY) production in brain tissue, which leads to decreased feed intake, increased energy expenditure, and lower body weight (Meier et al., 2004). Leptin also helps to inhibit anabolic pathways and assists in central catabolic pathways (Woods et al., 1998). The concentration of circulating leptin levels in cattle has been associated with increased fatness of steers (Ji et al., 1997; Chillard et al., 1998; Minton et al., 1998). Frühbeck (2001) also stated that as circulating leptin levels increase, appetite decreases. An animal with low fat stores typically has decreasing quantities of circulating leptin, followed by increasing appetite. However, Nkrumah et al. (2007) found that Angus-sired

steers had higher circulating serum leptin levels than Charolais-sired steers (20% higher), and that steers with higher leptin levels had higher DMI and higher RFI. Serum leptin had a positive phenotypic correlation with backfat (r = 0.41), carcass marbling (r = 0.28), and yield grade (r = 0.32). Serum leptin had a negative phenotypic correlation with *longissimus* muscle (LM) area (r = -0.17) and lean meat yield (r = -0.38). Angus bulls have been reported to have greater circulating leptin (3.0 ng/mL) than Brahman bulls (1.8 ng/mL), which could correspond with the breed's ability to deposit fat (Thomas et al., 2002; Nkrumah et al., 2007). Delavaud et al. (2002) reported a large difference between fat and lean cattle in leptin serum levels of Charolais and Holstein cattle. Fat Charolais had 6.6 ng/mL, fat Holstein had 13.7 ng/mL and lean Holstein had 3.7 ng/mL. Nkrumah et al. (2005) studied the polymorphisms in the bovine leptin (*LEP*) promoter and evaluated hybrid cattle from 3 composite lines. Beef Synthetic 1 contained 33% Angus, 33% Charolais, 20% Galloway and the remaining percentage was comprised of other beef breeds. Beef Synthetic 2 was composed of 60% Hereford and 40% other beef breeds. Dairy X Beef Synthetic was 60% dairy breeds (Holstein, Brown Swiss, or Simmental) and the remaining 40% comprised of Angus and Charolais. Animals with a TT genotype for a C/T substitution (UASMS2) at position 528 of the *LEP* 5'UTR (Genbank accession AB070365) had higher feed intake, growth rate, metabolic body weight, and live weight at slaughter. Animals with the TT genotype produced more leptin (91.40 ng/mL) than other genotypes (CC = 85.13 ng/mL and CT = 87.51ng/mL).

2.3c Ghrelin

Ghrelin is an important physiological regulator of feeding behavior and energy equilibrium because its function is to send information to the hypothalamus and stimulate appetite. Ghrelin also increases use of carbohydrates, reduces fat utilization, and increases gastric motility and acid secretion (Meier et al., 2004). Meier et al. (2004) also stated that circulating plasma ghrelin concentrations increased two-fold before a meal and dropped off to trough levels within one hour after feeding. Salfen et al. (2004) found that hogs that received ghrelin treatments had greater weight gain over the 5 day treatment period than hogs that were given saline treatments (0.57 kg vs. 0.21 kg). Even though the ghrelin-treated pigs had heavier body weights, they did not have an increase in feed intake. Conversely, Sun et al. (2003) created *GHRL*-null mice to determine the effect of ghrelin on dietary intake, but the *GHRL* -null mice did not differ from their wild-type littermates in food intake, behavior, reproduction, and size. The deletion of ghrelin was predicted to create anorexic mice that were much smaller in size as their desire for food would have been greatly reduced. However, this was not the case as both types of mice were similar in phenotype. The authors also noted that the *GHRL* -null mice responded to exogenous ghrelin treatments with an increase in appetite. This could mean that a compensatory mechanism allowed the animals to overcome ghrelin deficiency. Further study in this mouse model also indicated that *LEP* and *GHRL* function independently. When Wertz-Lutz et al. (2006) investigated the relationship between plasma ghrelin and feed intake and the hormones associated with nutritional

states of beef cattle, they found greater plasma ghrelin concentrations in steers that had feed withheld than steers that were fed (690 and 123 ± 6.5 pg/mL, respectively).

2.3d Neuropeptide Y

Neuropeptide Y was first isolated from porcine brain tissue by Tatemoto et al. (1982) and is a 36 amino acid peptide that is found in the central, peripheral, and enteric nervous systems in many species. Sundler et al. (1983) demonstrated that nerve fibers that were immune-reactive to neuropeptide Y were observed in the mucosal, submucosal and musculararal tunics of the small intestine of rats. Woods et al. (1998) adduced that NPY is associated with a positive state of energy and increased fat storage. Administration of NPY has been reported to increase energy intake, decrease energy expenditure, and increase lipogenesis. Levine and Morely (1984) and Clark et al. (1984) both showed that the administration of NPY increased feed intake in satiated rats. Neuropeptide Y has been administered to sheep (Miner et al., 1989), mice (Morley et al., 1987), ground squirrels (Nizielski et al., 1985), dogs (Pappas et al., 1986), and pigs (Pappas et al., 1986). Across all these studies, an increase in ingestive behavior was associated with the administration of NPY. Miner et al. (1990) repeated the experiment with NPY administration in sheep to determine impact on feed intake, and found the same results where both feed and water intake increased following injection of NPY.

2.3e Insulin-like Growth Factor I

Growth can be defined as the normal expansion of size as produced of tissues similar in constitution to that of the original (Gerrard and Grant, 2007). Growth can be achieved by both cell proliferation and enlargement (Gerrard and Grant, 2007). Insulin-

like growth factor I (IGF1) is a polypeptide hormone that regulates growth and cellular metabolism (Davis and Simmen, 2006). Circulating IGF1 is created and secreted by the liver. In mice, the deletion of the *IGF1* gene resulted in severe growth retardation (Sjorgen et al., 1999). Insulin-like growth factor 1 actively stimulates glucose metabolism and protein synthesis, and Baxter (1986) concluded that IGF1 influences the body in an autocrine/paracrine manner rather than an endocrine manner. Davis and Simmen (1997) found direct additive genetic correlations of circulating IGF1 with BW and BW gains that ranged from -0.21 to -0.54 and averaged -0.38 in lines of beef cattle that were divergently selected for serum IGF1 concentration. Serum IGF1 concentration has been used as a measure of selection for feed efficiency in Australia and the United States in research herds. The implementation of the use of serum levels of IGF1 as a selection criterion in breeding programs has been slow as there have been conflicting results reported. Moore et al. (2005) and Kahi and Hirooka (2007) have reported a significant correlation between RFI and circulating IGF1 concentration. However Lancaster et al. (2008) used Angus bulls and heifers that were selected from divergent lines for IGF1 concentration and found minimal correlation between RFI and IGF1 in heifers, while bulls that were in the low IGF1 selection line had numerically lower RFI than bulls of the high IGF1 selection line. Wood et al. (2002) showed within a simulation for genetic and economic evaluation that the use of IGF1 as a selection criterion in beef cattle could increase profitability of selection decisions and can be best put to use as a screening test to be identify animals to be placed into RFI tests in a two-stage selection program.

2.4 Organ Weights and Measures of Feed Efficiency

An area of research to help understand the biological variation of RFI has been to study relationships between organ weights of the digestive system and measures of feed efficiency. Splanchnic tissues have been of interest as they are approximately 4 to 6% of body mass but they utilize approximately 45% of total ATP utilization (Kelly and McBride, 1990; Caron et al., 2000). Mader et al. (2009) investigated the relationship between organ mass and feed efficiency on crossbred steers of Angus, Simmental, Charolais and Piedmontese genetic background. These steers had dams that were crossbred with mainly Angus and Simmental backgrounds and sires that were Angus, Simmental, crossbred (Angus X Simmental), Charolais and Piedmontese. They found that RFI was positively correlated with kidney fat weight ($r = 0.34$). Gain:feed ratio had a negative correlation with total visceral weight ($r = -0.44$) and visceral fat ($r = -0.41$) but had a positive correlation with spleen weight ($r = 0.30$). The correlation between RFI and total viscera weight was $r = 0.18$ and between RFI and gastrointestinal weight was $r = 0.05$. These weak correlations were not statistically significant. There were no significant correlations between RFI and individual tissue weights (liver, kidney, spleen, lung, reticulo-rumen, omasum, abomasums, small intestine, cecum, colon, visceral fat, length of small intestine, length of colon, and pancreas). However, a trend was observed between heart weight and RFI with a correlation of ($r = -0.24$) (Mader et al., 2009). Pitts (1951) evaluated guinea pigs and found that an increase in size of heart, liver, and kidneys were found in animals with leaner body composition. Kraybill et al. (1954) worked with Hereford cattle and found similar results to Pitts (1951).

The impact of individual hormones on measures of feed efficiency has been frequently described in the literature. An association with RFI has been demonstrated for concentrations of NPY (Levine and Morely, 1984), LEP (Nkrumah et al., 2007), GHRL (Salfen et al., 2004), and IGF1 (Moore et al., 2005). These studies have focused on the circulating levels of these hormones, but little information about their genotypes or level of expression, particularly in *Bos indicus* influenced cattle, has been reported. Furthermore, their relationships with a new measure of feed efficiency, MPRC, have not been investigated. Also, very little information exists about visceral organ size or weight and the relationships involving organ size and feed efficiency with carcass traits.

As a result, the objectives of this project were to: (1) investigate gene breed types for *IGF1*, *LEP*, *NPY*, and *GHRL* for their influence on feed efficiency (MPRC), visceral organ weights and carcass traits, (2) investigate the gene expression of *IGF1* and *LEP* in liver samples from animals previously identified to be divergent in feed efficiency (MPRC) and investigate potential relationships of gene expression with visceral organ weight and carcass traits, and (3) evaluate correlations of MPRC, organ weights and carcass traits in F_2 *Bos indicus-Bos taurus* steers produced in Cycle I of the McGregor Genomics Project.

3. MATERIALS AND METHODS

3.1 Animals

All procedures involving animals were approved by the Texas A&M University Institutional Animal Care and Use Committee (AUP 2002-116, 2005-147 and 2008-234). Animals utilized in this study were F_2 Nellore-Angus steers produced in full sib, embryo transfer families and from contemporary groups born in spring and fall calving seasons of 2003 through 2007 (referred to as Cycle I of the McGregor Genomics Project). The steers were produced from 13 Nellore-Angus F_1 donor females and 4 Nellore-Angus F_1 sires through embryo transfer. All F_1 parents were Nellore-sired. Steers were fed in pens of 4 using a Calan gate system to measure feed intake. Diet and feeding schedule are more fully described in (Amen, 2007). The average age of the steers when they were placed on feed was 11 to 13 months. Steers were fed *ad libitum* until they were harvested at 17 to 18 mo of age. Liver, heart, spleen, and viscera weights were collected at harvest immediately following evisceration, with liver samples obtained immediately thereafter. The liver samples were snap-frozen and stored at -70ºC until later analyses. Viscera weight refers to the GI tract weight including digesta; empty viscera weights were not taken. Animals were held without feed for approximately 18 hours prior to harvest, but had *ad libitum* access to water.

3.2 Determination of Gene Breed Type for Genes of Interest

Genes of interest were selected based on their roles in appetite suppression, activation, glucose metabolism, and lipogenesis as reported in the literature. For the

genes of interest (*GHRL*, *IGF1*, *LEP*, and *NPY*), human protein sequence was obtained from UniProt (http://www.uniprot.org/) and aligned to build Btau4.0 of the bovine genome sequence (The Bovine Genome Sequencing and Analysis Consortium, 2009) using BLAT (Kent, 2002) at University of California – Santa Cruz to identify the coordinates of bovine orthologs. Cattle in this project had previously been genotyped with the Illumina BovSNP50v1 chip. Genotypes for animals for single nucleotide polymorphisms (SNP) spanning a 1Mb region (or 2Mb for *NPY* and 4Mb for *IGFI* in family 77) centered on each candidate gene were extracted for the McGregor Genomics database. Data were filtered if completion rate for the SNP was < 90%, completion rate for the animal was < 90%, and minor allele frequency was < 0.05. After filtering, data were formatted for analysis of phase using fastphase software (Scheet and Stephens, 2006). Analysis was completed using 10 starts and runs of the expectation-maximization algorithm (Clare Gill, pers. comm.). Resultant gene breed types were manually assigned by following the Nellore and Angus haplotypes from the grandparental generation through the three-generation pedigree. Thus, each gene for each animal was assigned a gene breed type as Angus (AA), Angus-Nellore (AN), Nellore-Angus (NA) or Nellore (NN), where the sire is listed first followed by the dam.

3.3 Calculation of Model Predicted Residual Consumption and Efficiency Group Classification

Daily feed intake was predicted based on the NRC (2000) model and as described in Amen (2007). Standardized inputs included animal type, age, gender, condition, and breed to calculate MPRC for each animal (Amen, 2007). Animals that

had a negative MPRC value were considered efficient (as with RFI) because they had consumed less feed than predicted for a relative rate of weight gain. Model predicted residual consumption was used instead of RFI because MPRC may be better for evaluation across contemporary groups because its mean is not forced to be zero in each group (and metabolic weight and weight gain can be given different weightings in different contemporary groups) and because previous analyses showed more informative differences in MPRC than RFI (Amen, 2007). This raw MPRC value was used in the entire 232-animal data set.

After calculating MPRC for the 180 animals that were available at the time (Amen, 2007), a mixed model that included fixed effects of sire and family nested within sire was used to calculate MPRC residuals. These residuals were then sorted from highest to lowest. From these 180 animals, 54 animals were selected for additional analyses based on their respective MPRC residual value that included 18 animals from each tail of distribution and 18 animals clustered around the average. Animals that resided in the left (negative) tail were assigned an efficient classification, while animals in the right tail were assigned an inefficient classification, and animals that surrounded the average were ascribed an average classification. This 54-animal subset was described by Kochan et al. (2009) and was used for RNA extraction and evaluation by real time quantitative RT-PCR (qRT-PCR).

3.4 RNA Extraction and Real Time Quantitative RT-PCR for 54-Animal Subset

Tissue samples obtained post-harvest were pulverized in liquid nitrogen with a mortar and pestle. Tissues were transferred and homogenized in 1 mL of Tri-reagent

(TRI) with an 18 ga needle (Life Technologies, Carlsbad, CA). After tissue was completely homogenized, the contents were transferred into a tube with 200 µl of 1-bromo-3-chloro-propane (BCP) (Sigma, St. Louis, MO, USA). Samples were then centrifuged for 10 minutes at 14,000*g* under 4ºC. The supernatant was removed and transferred into a tube with 400 µl of TRI reagent and 200 µl BCP. After mixing well by inverting the tube the samples were again centrifuged for 10 minutes at 14,000*g* under 4ºC. The supernatant was obtained and placed in a clean tube containing 200µl BCP, which was then mixed well by inversion. The samples were centrifuged for a final time at the previous settings. The manufacturer's recommended protocol was amended to include additional extractions with 2:1 TRI: BCP and BCP alone (Kochan et al., 2009). After TRI and BCP extractions, the RNA was precipitated in isopropanol for a minimum of 2 hours. The samples were washed consecutively with 70%, 95%, and 100% ethanol and then resuspended in 100 µl nuclease-free water (Life Technologies, Carslbad, CA). Total RNA quality was assessed by capillary electrophoresis on an RNA 6000 NanoChip with a 2100 Bioanalyzer (Agilent Technologies, Palo Alto, California). Samples with an RNA Integrity Number (RIN) less than 8.0 were not used. Total RNA was purified through RNeasy mini columns (Qiagen, Valencia, CA, USA) according to the manufacturer's protocol. Samples were then DNase-treated with the DNA-*free* kit (Life Technologies, Carlsbad, CA). Samples were quantified on a NanoDrop 1000 spectrophotometer (Thermo Scientific, Waltham, MA, USA). After quantification, all samples were diluted in nuclease free water to 80 ng/µl to standardize concentrations.

Reverse transcription (RT) of 2 µg of total RNA was carried out in 25 µl reactions. RNA was primed with gene specific primers and reverse transcribed with the ABI High-Capacity kit cDNA Reverse Transcription Kit (Applied Biosystems, Foster City, CA, USA) for RT-PCR. For a single 25 µl reaction the following amounts of materials were added: 2.5µl RT Buffer, 0.75µl of each reverse primer (*IGF1, LEP, COX6A1, COX7A2* (Kochan et al., 2009)), 1µl dNTP, 4.3 µl of nuclease free water, 1µl of RT enzyme, and 13.2 µl of sample. Complementary DNA was then used for qRT-PCR with SYBR® GreenER PCR mix (Life Technologies, Carlsbad, CA) in a 20 µl reaction in 384-well optical PCR plate format with technical triplicates. The primer set for *IGF1* amplifies a 117-bp product (F-Primer: 5' CAGCAGTCTTCCAACCCAA; R-Primer: 5' AAGGCGAGCAAGCACAG). Reverse transcriptase-PCR reactions were carried out in 384-well plates on an Applied Biosystems 7900HT Sequence Detection System (Life Technologies, Carslbad, CA) using default 9600 emulation cycling parameters.

Relative expression of *IGF1* was calculated as described in Livak and Schmittgen (2001). Cytochrome c oxidase subunit 6A1 (COX6A1) was used as a reference gene for normalization. The average expression of the average efficiency group was used as the calibrator.

3.5 Statistical Analyses

Carcass traits and organ weight data were analyzed for 2 groups of animals: (1) the 54 F_2 Nellore-Angus steers described by Kochan et al. (2009) that were identified to be divergent for MPRC residual ratings and (2) the complete data set of 232 F_2 Nellore-

Angus steers produced in Cycle I of the McGregor Genomics Project (including the 54-steer subset). Amen (2007) had previously evaluated the first 180 of these steers. In all analyses $P < 0.05$ was the significance level used to decide differences, but trends with $P < 0.10$ were also evaluated.

General linear model procedures were used for multiple initial analyses in both the 54-steer subset and the complete 232-steer dataset. Several analyses with single factor models were used to evaluate the influence of gene breed type (individually for *IGF1, LEP, NPY, and GHRL*) on MPRC, organ weights and carcass traits in both the 54- and 232-steer data sets. Additionally, multiple factor analyses to evaluate gene breed type, and contemporary group were also conducted for the 232 F_2 steers. When gene breed type was significant, structured contrasts were investigated to compare heterozygotes to homozygotes, alternate heterozygotes, and maternal (AA and NA vs. AN and NN) or paternal (AA and AN vs. NA and NN) line of inheritance.

The influence of each gene breed type (*IGFI, LEP, NPY,* and *GHRL),* contemporary group and efficiency group on *IGFI* RQ were evaluated in preliminary single factor models for the 54-subset. The final statistical model included sire and *IGFI* gene breed type nested within sire.

Pearson correlations among the organ weights, carcass traits, and MPRC values were evaluated in both the 54- and 232-animal datasets, and, correlations of these traits with *IGF1* were also evaluated in the 54-steer subset.

4. RESULTS AND DISCUSSION

The data in this section are presented where analyses of the 54-animal subset used for quantitative RT-PCR are presented first, followed by gene breed type analyses of the entire set of 232 Cycle I steers.

4.1 Analyses of 54-Animal Subset

4.1a Gene Breed Type Assignment for Candidate Genes

For each candidate gene (*IGFI, NPY, GHRL*, and *LEP*) a gene breed type was generated for each individual. Gene breed type was initially assigned based on haplotypes of 12 SNP for *IGF1*, 6 SNP for *NPY*, 19 SNP for *GHRL*, and 14 SNP for *LEP*. In family 77 for *IGFI* there was a rare situation where both parents had identical SNP haplotypes. Thus parent of origin of the Nellore and Angus alleles for heterozygotes could not be identified with certainty. As a result, the region for SNP detection around the *IGFI* gene was increased to 4 Mb for family 77 so that parent of origin could be differentiated. Assignment of gene breed type for *NPY* also presented some difficulty as only 6 SNP were located in the 1 Mb region around this gene of interest. Multiple genotyping errors were unable to be resolved due to the small number of SNP. As a result, a 2 Mb region around *NPY* was generated, and an additional 10 SNP were added to the haplotypes. These SNP still had to meet the previous criteria of the first set of SNP. There were no difficulties in assigning *GHRL* or *LEP* gene breed types from 1 Mb regions around these genes. The distribution of gene breed types across efficiency groups is displayed in Table 1.

Table 1. Distribution across efficiency groups of *LEP*, *GHRL*, *NPY*, and *IGF1* gene breed type among 54-animals evaluated on MPRC residual values

	Gene breed type[1]				
Efficiency group	AA[1]	AN	NA	NN	Totals
LEP					
Efficient	3	2	3	8	18
Average	6	3	4	5	18
Inefficient	3	6	6	3	18
GHRL					
Efficient	5	6	4	3	18
Average	6	3	5	3	18
Inefficient	4	3	4	7	18
NPY					
Efficient	6	3	4	5	18
Average	4	3	4	6	17
Inefficient	5	3	7	3	18
IGFI					
Efficient	4	6	3	4	17
Average	1	3	3	10	17
Inefficient	5	5	4	1	15

[1]Breed of origin of haplotype from sire is listed first (A = Angus; N = Nellore)

In addition to generating gene breed types for each candidate gene, single factor analyses were run on viscera and organ weights, MPRC, and carcass traits on the 54-animal subset. Tables 2 and 3 present significance levels for the single factor analyses of gene breed type for MPRC, organ and viscera weights and carcass traits in the 54-animal subset.

Table 2. Significance levels from single factor analyses of gene breed type for MPRC, organ and viscera weights in 54-animal subset

	MPRC	Liver	Spleen	Heart	Viscera
GHRL	0.34	0.69	0.83	0.44	0.62
LEP	0.72	0.95	0.21	0.75	0.15
IGFI	0.81	0.57	0.32	0.61	0.87
NPY	0.73	0.86	0.05	0.75	0.97

[1]MPRC= model predicted residual consumption

Table 3. Significance levels from single factor analyses of gene breed type for carcass traits in 54-animal subset

	MARBL	MARBR	FT	ADJFT	REA	KPH	HCW	YG
GHRL	0.14	0.17	0.10	0.43	0.97	0.01	0.50	0.14
LEP	0.60	0.85	0.95	0.98	0.19	0.34	0.30	0.81
IGF1	0.71	0.78	0.76	0.55	0.89	0.24	0.55	0.65
NPY	0.12	0.23	0.06	0.03	0.27	0.15	0.60	0.07

[1]MARBL and MARBR denote the amount of marbling in the left and right side of the carcass. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness; ADJFT= adjusted fat thickness; HCW = hot carcass weight; KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area

For the 54-animal subset, there were no significant gene breed type effects for MPRC, liver weight, heart weight, viscera weight, MARBL, MARBR, REA, or HCW. However, the *GHRL* gene breed type was significant for KPH. *G*ene breed type for *NPY* was significant for ADJFAT and spleen weight. *NPY* gene breed type also approached significance for FT and YG.

4.1b Relative Expression of Insulin-like Growth Factor 1

Expression of *IGF1* was calculated by the relative quantity (RQ) method as described in Schmittgen and Livak (2008) where relative gene expression data of the gene of interest (GOI) is presented relative to a calibrator. Preliminary analyses of *IGFI* RQ included using a general linear model with single factors of contemporary group, family and gene breed types of individual genes (*GHRL*, *LEP*, *IGFI* and *NPY*). In the initial single factor analyses of *IGF1* RQ, contemporary group ($P = 0.11$, $R^2 = 0.17$), family ($P = 0.33$; $R^2 = 0.24$), and individual gene breed types were not significant.

Subsequent analyses of *IGFI* RQ including efficiency group and *IGFI* gene breed type nested within efficiency group in the model accounted for 23% of the variation. The final model included sire and *IGFI* gene breed type nested within sire, which accounted for 29% of the variation in *IGFI* RQ. Least squares means of *IGFI* RQ across sires are presented in Table 4. Least squares means for *IGF1* RQ from the model that included efficiency group and *IGF1* gene breed type nested within efficiency group are reported in Table 5.

Table 4. Least squares means for *IGF1* RQ across sires from the model including sire and *IGF1* gene breed type nested within sire

Sire	N	Means
297J	8	1.46 ± 0.30^{a}
432H	8	$1.15 \pm 0.30^{a,b}$
437J	13	0.56 ± 0.26^{b}
551G	20	$1.16 \pm 0.22^{a,b}$

Least squares means with differing superscripts differ ($P < 0.05$).

Table 5. Least squares means for *IGFI* RQ across efficiency group from the model including efficiency group and *IGFI* gene breed type nested within efficiency group

Efficiency Group	n	Means
Average	16	1.46 ± 0.22^{a}
Efficient	17	$0.88 \pm 0.20^{a,b}$
Inefficient	16	0.60 ± 0.26^{b}

Means with differing superscripts differ ($P < 0.05$).

IGFI RQ value was significantly higher in the Average group than in the Inefficient group, but no difference was detected between the Inefficient and Efficient group. In catfish that had been identified from slow or fast growing families, *IGFI* mRNA was measured in fast muscle, located under the dorsal fin, and liver. The catfish family that had the poorest feed conversion ratio and growth rate did not differ from the family that had the highest growth rate and best feed conversion ratio in *IGFI* mRNA levels from the liver or fast muscle (Peterson et al., 2004). Even though the catfish were not broken down into efficiency group like the cattle were in this study (they were selected on growth rate and feed efficiency), the results suggest that there might be no difference between *IGFI* mRNA expression between the efficiency groups in cattle. The biological reason why the Average group would be different from the other two groups is unclear; interpretation of the means in the current study must also consider that the Average group contained one individual that was an apparent outlier.

The *IGFI* gene expression was highly variable, and is shown in Figure 1,

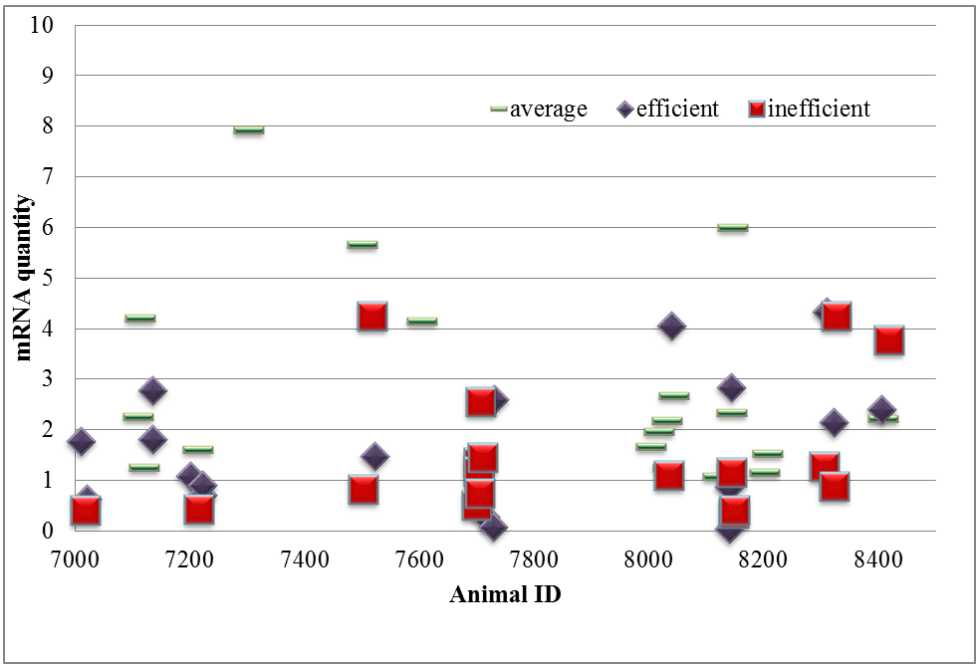

Figure 1. Relative quantities of IGFI mRNA

The efficiency of the *IGFI* primer set was 99.5%. This large degree of variability may be due to *IGF1* mRNA not being related to this measure of feed efficiency. There was also one individual in the Average group whose expression was considerably higher than the others and likely influenced comparisons of means across groups.

4.1c Correlations of IGF1 RQ Values With Carcass Traits and Organ Weights

Correlations between *IGFI* RQ and MPRC, carcass traits and organ weights are shown in Table 6. *IGFI* RQ showed a negative correlation to liver weight ($r = -0.23$) that approached significance ($P = 0.09$). The negative correlation between *IGFI* RQ and liver weight seems unusual as the liver is the primary tissue for *IGFI* production (Carter et al., 2002). Van Buul-Offers et al. (1986) administered growth hormone that was derived from *Escherichia coli* to Snell dwarf mice. After 4 weeks of treatment the mice were killed and body weights and muscle weights were measured. Liver weights from control mice (409 ± 18 mg) were significantly different from those of mice that received the IGFI treatment (581 ± 30 mg; van Buul-Offers et al., 1986). These results indicate that as the amount of IGFI increases, liver size is expected to increase. However, the correlation between *IGF1* RQ and liver weight in the current study may suggest the opposite is true in cattle. The differences between the findings of this study and van Buul-Offers et al. (1986) could be attributed to the fact that in this study, mRNA was measured, whereas in the study by van Buul-Offers et al. (1986) organ weights were measured after IGFI protein had been administered to the mice. Liver concentration of *IGF1* mRNA may not be directly correlated with circulating IGF1 concentration. Also,

the individual observation that was an apparent outlier in the Average group must be considered.

Rosselot et al. (1995) examined the effects of exogenous chicken growth hormone (cGH) administration on *IGFI* gene expression in chickens. The cGH was administered by 2 methods; continuous infusion and pulsatile infusion. Peptide levels for IGF1 and *IGFI* mRNA levels were shown to have no statistically significant correlation in heart, kidney, spleen, gastrocnemius muscle, pectoralis muscle, or liver tissue except when the cGH was administered in a pulsatile fashion and the mRNA was extracted from liver tissue. The authors suggested that the reason for the lack of symmetry in *IGFI* mRNA expression and peptide levels is due to organ specific regulation and function. The relationship between serum levels of IGFI and *IGFI* RQ were not evaluated in this study but should be investigated.

Table 6. Correlations between *IGF1* RQ and MPRC, organ weights, and carcass traits of 54 steers[1]

	MPRC	Heart	Liver	Spleen	Viscera	HCW	REA	ADJFT	MARBR	MARBL	YG	KPH
IGF1 RQ	0.02	-0.07	-0.23	0.20	-0.14	-0.05	-0.05	-0.06	-0.04	-0.05	-0.03	-0.14
	0.83	0.64	0.09	0.15	0.30	0.70	0.71	0.65	0.76	0.69	0.82	0.31

[1]Top value is r with *P*-value below. MPRC = model predicted residual consumption. MARBL and MARBR denote the amount of marbling in the left and right side of the carcass, respectively. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness; ADJFT= adjusted fat thickness; HCW = hot carcass weight; KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area

4.1d Model Predicted Residual Consumption (MPRC) Residuals

Multiple analyses of model predicted residual consumption (MPRC) residuals were evaluated in the 54-steer subset. The mean MPRC in the 54-steer subset was -0.02 kg, which indicates that the animals ate 0.02 kg less per day than the predicted intake from the NRC model. In preliminary analyses, efficiency group ($R^2 = 0.94$) and contemporary group ($R^2 = 0.63$) were both significant ($P < 0.001$) for MPRC differences.

It was expected that efficiency group would account for large differences in MPRC, as the data were structured that way; however, contemporary group also accounted for large differences in MPRC (R^2 of 0.63). This could be attributed to the Spring 2005 contemporary group having 15 efficient animals (almost the entire group of efficient animals) as animals were classified into efficiency groups based on MPRC value without respect to contemporary group, and this particular contemporary group was identified as being more efficient than several others (Amen, 2007). Table 7 shows the distribution of efficiency groups across birth year season in these 54 steers.

Table 7. Distribution of contemporary group by efficiency group in 54 steers

	Efficiency group			
	Average	Efficient	Inefficient	Totals
Spring 2003	1	1	1	3
Fall 2003	3	0	5	8
Spring 2004	4	1	2	7
Fall 2004	4	1	4	9
Spring 2005	2	15	0	17
Fall 2005	4	0	6	10
Totals	18	18	18	54

4.1e Correlations among MPRC, Organ Weights, and Carcass Traits

Summary statistics are provided for MPRC, organ weights and carcass traits in Table 8 for the 54-steer subset; correlations involving carcass traits are presented in Table 9, and correlations involving MPRC, organ weights, and carcass traits are presented in Table 10.

Table 8. Summary statistics for carcass traits and organ weights for 54-animal subset

Trait	n	Mean	SD	Minimum	Maximum
MPRC residual[1] (kg/d)	54	-0.02	1.95	-3.62	3.24
Fat thickness (cm)	54	1.24	0.38	0.51	2.41
Ribeye area (cm^2)	54	73.13	6.11	63.20	89.00
Hot carcass weight (kg)	54	309.73	27.57	256.36	368.18
Adj. fat thickness (cm)	54	1.34	0.43	0.50	2.54
Marbling right[2]	51	400.20	81.06	310.00	670.00
Marbling left[2]	54	400.37	79.12	310.00	650.00
Yield grade	54	3.307	0.55	1.90	4.80
Spleen weight (kg)	54	0.87	0.12	0.50	1.18
Viscera weight (kg)	53	68.00	9.17	49.45	89.81
Liver weight (kg)	54	5.11	0.64	3.76	6.59
Heart weight (kg)	47	1.64	0.25	1.01	2.18

[1]Model predicted residual consumption residual values pre-adjusted for family(sire)
[2]400 = Small00. The right carcass side was electrically stimulated; the left side was not stimulated

Table 9. Correlations between carcass traits among of 54-animal subset

	MARBL	FT	ADJFAT	REA	KPH	HCW	YG
MARBR	0.88	0.26	0.32	-0.17	0.02	-0.05	0.35
	<0.001	0.07	0.009	0.22	0.85	0.72	0.01
MARBL		0.22	0.35	0.15	0.08	0.04	0.41
		0.10	0.009	0.26	0.56	0.76	0.002
FT			0.92	0.22	0.21	0.37	0.78
			<0.001	0.11	0.13	0.006	<0.001
ADJFAT				0.24	0.28	0.35	0.84
				0.08	0.04	0.009	<0.001
REA					0	0.57	-0.12
					1	<0.001	0.39
KPH						0.14	0.54
						0.30	<0.001
HCW							0.40
							0.002

[1]Top value is r, and bottom value is *P*-value. MARBL and MARBR denote the amount of marbling in the left and right side of the carcass. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness; ADJFT= adjusted fat thickness; HCW = hot carcass weight; KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area

Table 10. Correlations between MPRC, organ weights, and carcass data of 54-animal subset

	MPRC	Liver	Heart	Viscera	MARBR	MARBL	FT	ADJFAT	REA	KPH	HCW	YG
Spleen	0.02	-0.11	0.08	-0.13	-0.14	-0.11	0.08	0.11	0.04	-0.17	-0.03	-0.02
	0.87	0.44	0.58	0.34	0.31	0.44	0.53	0.43	0.75	0.21	0.78	0.91
MPRC		-0.21	-0.01	-0.29	0.32	0.36	0.02	0.05	-0.33	0.09	0	0.23
		0.13	0.90	0.03	0.02	0.007	0.90	0.73	0.01	0.49	0.96	0.09
Liver			0.61	0.13	-0.24	-0.24	0	-0.01	0.39	0.03	0.62	0.03
			0.0001	0.34	0.08	0.08	0.97	0.89	0.003	0.84	0.0001	0.83
Heart				-0.18	-0.11	-0.17	-0.18	-0.26	0.16	0.06	0.45	-0.08
				0.23	0.48	0.26	0.22	0.08	0.29	0.68	0.001	0.58
Viscera					-0.09	-0.03	-0.18	0.20	-0.01	-0.04	0.09	-0.11
					0.52	0.82	0.19	0.16	0.94	0.75	0.53	0.42

[1]Top value is r, and bottom value is *P*-value. MARBL and MARBR denote the amount of marbling in the left and right side of the carcass. MPRC = model predicted residual consumption. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness; ADJFT= adjusted fat thickness; HCW = hot carcass weight; KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area

Viscera weight (r = -0.29; *P* = 0.03), MARBR (r = 0.32; *P* = 0.02), MARBL (r = 0.36; *P* = 0.007), and ribeye area (r = -0.33; *P* = 0.01) all had significant correlations with MPRC. Within the individual organ weights, liver weight and heart weight (r = 0.61; *P* = 0.0001) had a strong, positive correlation. MARBR had statistically significant correlations with MARBL (r = 0.88), adjusted fat thickness (r = 0.32) and yield grade (r = 0.35). MARBL was also significantly correlated with adjusted fat thickness (r = 0.35) and yield grade (r = 0.41). Fat thickness was significantly correlated to adjusted fat thickness, hot carcass weight (r = 0.37) and yield grade (r = 0.78). Adjusted fat thickness had a strong correlation with yield grade (r = 0.84; *P* = <0.001), a moderate correlation with hot carcass weight (r = 0.35; *P* = 0.009), and a weak correlation with kidney pelvic heart fat (r = 0.28; *P* = 0.04). Ribeye area was significantly correlated with hot carcass weight (r = 0.57). Kidney pelvic heart fat and hot carcass weight were also significantly correlated with yield grade (r = 0.54; r = 0.40).

4.2 Analyses of 232 Cycle I F_2 Steers

4.2a Gene Breed Type Assignment for Candidate Genes

The method of assigning the gene breed types for the 4 candidate genes in the 232-animal data set followed the same procedure as described in the 54-animal subset. Table 11 describes results from the single factor analyses of gene breed type for MPRC, organ, and viscera weights, and Table 12 describes the results from single factor analyses for carcass traits. For these analyses, gene breed type was the only independent variable in the model.

Table 11. Significance levels due to gene breed effects from single factor analyses for MPRC[1] organ and viscera weights for 232-animal data set

	MPRC	Liver	Spleen	Heart	Viscera
GHRL	0.64	0.08	0.41	0.30	0.01
LEP	0.34	0.07	0.41	0.28	0.16
IGFI	0.27	0.34	0.52	0.82	0.26
NPY	0.32	0.05	0.46	0.47	0.72

[1]MPRC= model predicted residual consumption

Table 12. Significance levels due to gene breed effects from single factor analyses for carcass traits for 232-animal data set

	MARBL[1]	MARBR	FT	ADJFAT	REA	KPH	HCW	YG
GHRL	0.45	0.69	0.22	0.24	0.41	0.05	0.92	0.15
LEP	0.96	0.98	0.83	0.68	0.03	0.82	0.01	0.87
IGFI	0.87	0.98	0.97	0.95	0.65	0.09	0.29	0.25
NPY	0.50	0.57	0.70	0.58	0.38	0.91	0.07	0.73

[1]MARBL and MARBR denote the amount of marbling in the left and right side of the carcass. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness; ADJFT= adjusted fat thickness; HCW = hot carcass weight; KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area

Among these steers, no candidate gene breed type differences were seen in MPRC, MARBL, MARBR, heart weight or spleen weight. The *NPY* gene breed type influenced liver weight, and *LEP* gene breed type approached significance for liver weight. Gene breed type of *IGF1* approached significance for KPH. Gene breed type for *LEP* affected REA and HCW. The *NPY* gene breed type approached significance for HCW and *GHRL* gene breed type was significant for viscera weight and KPH. The

GHRL gene breed type approached significance for liver weight. These results could mean that the differences between Angus and Nellore cattle for these traits are not substantial in regard to these genes, or that no performance differences existed in this particular population due to the gene breed types present.

Table 13. Least squares means for MPRC and organ weights by contemporary groups

	n	MPRC (kd/d)	Liver (kg)	Spleen (kg)	Heart (kg)	Viscera (kg)
S03[1]	23	$0.69 \pm 0.24^{b,c,d,e}$	$5.28 \pm 0.15^{b,c,d}$	0.77 ± 0.05	1.61 ± 0.07	$64.21 \pm 2.02^{b,c,d}$
F03	26	$1.05 \pm 0.22^{c,d,e}$	$4.70 \pm 0.14^{a,b,c}$	0.68 ± 0.05	1.49 ± 0.11	$60.25 \pm 1.94^{a,b,c}$
S04	35	$0.03 \pm 0.19^{a,b}$	$4.97 \pm 0.12^{a,b,c,d}$	0.81 ± 0.04	1.57 ± 0.04	$67.31 \pm 1.64^{c,d}$
F04	31	$-0.18 \pm 0.20^{a,b}$	$4.79 \pm 0.13^{a,b,c}$	0.67 ± 0.04	1.49 ± 0.04	$66.43 \pm 1.74^{c,d}$
S05	36	-1.64 ± 0.19^{f}	$5.15 \pm 0.12^{b,c,d}$	0.70 ± 0.04	1.55 ± 0.04	$65.68 \pm 1.61^{c,d}$
F05	30	$0.58 \pm 0.21^{b,c,d,e}$	$4.73 \pm 0.13^{a,b,c}$	0.76 ± 0.04	1.50 ± 0.04	$60.23 \pm 1.77^{a,b,c}$
S06	24	$-0.13 \pm 0.23^{a,b,d}$	$4.70 \pm 0.15^{a,b,c}$	0.71 ± 0.05	1.55 ± 0.05	$64.79 \pm 1.98^{b,c,d}$
F06	13	$0.26 \pm 0.31^{a,b,c,d}$	$4.90 \pm 0.20^{a,b,c,d}$	0.74 ± 0.07	1.61 ± 0.07	$65.94 \pm 2.80^{b,c,d}$
S07	14	$0.16 \pm 0.31^{a,b,c,d}$	$4.50 \pm 0.19^{a,b}$	0.70 ± 0.07	1.46 ± 0.06	$57.18 \pm 2.69^{a,b}$

[1] S03 denotes the season (S = spring; F = Fall) and birth year (03 = 2003, etc.) for the cattle in this study. Least squares means with differing superscripts differ ($P < 0.05$).

Table 13 describes results from single factor analyses for MPRC and organ weights, Table 14 describes results from single factor analyses for REA, YG, KPH, and HCW, and Table 15 describes results from single factor analyses for marbling, FT, and adjusted fat thickness. For these analyses, contemporary group was the only independent variable in the model.

Table 14. Least squares means for REA, KPH, YG, and HCW by contemporary group

	n	REA (cm^2)	KPH	YG	HCW (kg)
S03[1]	23	77.67 1.34^{d}	2.15 ± 0.12^{a,b,c,d}	3.01 ± 0.13^{a,b,c}	303.36 ± 7.05^{a,b,c,d,e}
F03	26	70.07 ± 1.26^{a,b}	2.19 ± 0.11^{a,b,c,d}	3.25 ± 0.12^{a,b,c}	285.20 ± 6.63^{a,b,c}
S04	35	72.48 ± 1.09^{a,b}	2.17 ± 0.01^{a,b,c}	3.04 ± 0.11^{a,b,c}	294.94 ± 5.71^{a,b,c,d}
F04	31	72.72 ± 1.16^{a,b}	2.94 ± 0.10^{e}	3.65 ± 0.11^{d}	309.18 ± 6.07^{b,c,d,e}
S05	36	72.31 ± 1.07^{d}	2.29 ± 0.09^{b,c,d}	3.27 ± 0.10^{b,c}	298.81 ± 5.63^{a,b,c,d,e}
F05	30	70.73 ± 1.18^{a,b,c}	2.26 ± 0.10^{b,c,d}	3.07 ± 0.11^{a,b,c}	298.62 ± 6.17^{a,b,c,d,e}
S06	24	70.99 ± 1.31^{a,c}	2.21 ± 0.12^{a,b,c,d}	3.25 ± 0.13^{a,b,c}	296.57 ± 6.90^{a,b,c,d,e}
F06	13	76.87 ± 1.79^{d}	2.50 ± 0.16^{b,c,d}	3.08 ± 0.17^{a,b,c}	317.97 ± 9.38^{c,d,e}
S07	14	68.39 ± 1.72^{a,b,c}	1.86 ± 0.15^{a,b}	2.86 ± 0.17^{a,b}	259.06 ± 9.03^{f}

[1] S03 denotes the season (S = spring; F = Fall) and birth year (03 = 2003, etc.) for the cattle used in this study. Least squares means with differing superscripts differ ($P < 0.05$).

Table 15. Least squares means for ADJFAT, FT, MARBL, MARBR by contemporary group

	n	ADJFAT	FT	MARBL	MARBR
S03[1]	23	1.47 ± 0.09^{b,c,d,e}	1.30 ± 0.09^{b,c,d,e,f}	410.43 ± 15.92^{b,d,e,f,g}	410.00 ± 15.79^{b,e,f}
F03	26	1.48 ± 0.09^{b,c,d,e}	1.28 ± 0.09^{b,c,d,e,f}	464.00 ± 15.27^{a,c,d,g}	460.38 ± 14.85^{a,c,d,g,h,i}
S04	35	1.33 ± 0.08^{a,b,c,d}	1.09 ± 0.07^{a,b,c,d,e}	405.43 ± 12.90^{b,c,d,e,f,g,i}	399.41 ± 13.00^{a,c,d,e,f,h,i}
F04	31	1.66 ± 0.08^{c}	1.48 ± 0.08^{c,e,f}	420.00 ± 13.71^{d,e,f,g}	426.25 ± 15.46^{b,c,d,f,h}
S05	36	1.47 ± 0.08^{b,c,d}	1.27 ± 0.07^{b,c,d,e}	374.72 ± 12.72^{a,c,d,g,h,i}	383.06 ± 12.62^{a,c,d,f,g,h,i}
F05	30	1.17 ± 0.08^{a,b}	1.03 ± 0.08^{a,b,c}	443.67 ± 13.94^{a,c,h}	428.33 ± 13.83^{a,c,g,i}
S06	24	1.37 ± 0.09^{b,c,d,e}	1.28 ± 0.09^{b,c,d,e,f}	372.08 ± 15.58^{b,e,f}	354.58 ± 15.46^{b,e,f}
F06	13	1.30 ± 0.13^{a,b,c,d}	1.22 ± 0.12^{a,b,c,d,e}	436.92 ± 21.17^{a,c,d,e,f,g,i}	429.23 ± 21.00^{a,c,d,e,f,h,i}
S07	14	1.23 ± 0.12^{a,b,c,d}	1.04 ± 0.12^{a,b,c,d,e}	351.00 ± 24.14^{a,c,g,h,i}	350.71 ± 20.24^{a,c,d,g,h,i}

[1] S03 denotes the season (S = spring; F = Fall) and birth year (03 = 2003, etc.) for the cattle used in this study. Least squares means with differing superscripts differ ($P < 0.05$).

Further analyses were conducted with both contemporary group and gene breed type incorporated into the model. Table 16 displays these results for the carcass traits and Table 17 displays the results for organ weights and MPRC. In single-factor analyses, *GHRL* gene breed type was significant for viscera weight and KPH. After including contemporary group into the model, *GHRL* gene breed type retained its significance for both viscera weight and KPH. Gene breed type of *LEP* also was significant when it was the only factor in the model for REA and HCW analyses, and it retained its statistical significance for these 2 traits when contemporary group was added to the model. Gene breed type for *NPY* was significant for liver weight as the sole model effect and remained significant when contemporary group was also considered. When the gene breed type remained significant after including contemporary group in the model, this indicates that the gene breed types likely have real effects on the above mentioned traits, and deserve further investigation.

Table 16. Significance levels due to gene breed type effects and contemporary group for carcass traits

	MARBL	MARBR	FT	ADJFAT	REA	KPH	HCW	YG
GHRL	0.556	0.881	0.317	0.494	0.178	0.102	0.829	0.242
	<0.001	<0.001	0.004	0.010	<0.001	<0.001	<0.001	0.002
LEP	0.814	0.989	0.827	0.678	0.054	0.850	0.043	0.927
	<0.001	<0.001	0.002	0. 002	<0.001	<0.001	0.004	0.007
IGFI	0.834	0.969	0.889	0.955	0.418	0.048	0.248	0.136
	<0.001	<0.001	0.011	0.021	<0.001	<0.001	<0.001	0.003
NPY	0.755	0.710	0.352	0.222	0.261	0.441	0.037	0.340
	<0.001	<0.001	0.001	0.002	<0.002	<0.001	<0.001	<0.001

[1]Top value is the *P* - value of gene breed type. Bottom value is the *P* -value of the contemporary group. MARBL and MARBR denote the amount of marbling in the left and right side of the carcass. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness (cm); ADJFT= adjusted fat thickness (cm); HCW = hot carcass weight (kg); KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area (cm^2)

Table 17. Significance levels[1] due to gene breed effects and contemporary group for MPRC and organ weights for the 232 data set

	MPRC	Liver	Spleen	Heart	Viscera
GHRL	0.477	0.020	0.473	0.205	0.019
	<0.001	0.002	0.684	0.364	0.004
LEP	0.378	0.058	0.292	0.351	0.273
	<0.001	0.005	0.584	0.844	0.042
IGFI	0.475	0.598	0.516	0.920	0.532
	<0.001	0.012	0.630	0.558	0.001
NPY	0.284	0.031	0.464	0.516	0.475
	<0.001	0.005	0.643	0.459	0.003

[1]Top value is the *P* -value of gene breed type. Bottom value is the *P*-value of the contemporary group.

For the traits where gene breed type was significant in the model that also included contemporary group, least squares means were generated. The least squares means for liver weight are reported in Table 18. For liver weight, the *GHRL* gene breed type that was the lightest was AN. However, the lightest gene breed type for *LEP* was NN, and the lightest gene breed type *NPY* was AN. For all three genes, the NA gene breed type was numerically higher than the AN gene breed type. For *GHRL*, the AN gene breed type was outside the range of the two homozygote gene breed types. *GHRL* was also the only gene where the 2 homozygotes differed statistically for liver weight. The mid parent value for *GHRL* was 4.90 kg, and the heterozygote average is 4.83 kg. These values did not differ significantly. This typically is thought to mean that there is no dominance effect. The mid parent value and heterozygote average also did not differ for *LEP* and *NPY* for liver weight. Additional structured contrasts were also conducted for the *GHRL*, *LEP*, and *NPY* gene breed types for liver weight to determine if the alternate heterozygotes differed from each other and if potential parent of origin effects (e.g. imprinting) occurred. For *GHRL* gene breed type, the alternate heterozygotes differed ($P = 0.002$) and the breed of the maternal haplotype differed ($P = 0.039$) as well. However, this difference appears to be entirely due to the difference between heterozygotes. The *LEP* alternate heterozygotes did not differ ($P = 0.249$) but the breed of the maternal haplotype did ($P = 0.011$). For the *NPY* gene breed type the alternate heterozygotes were statistically different and the breed of the maternal haplotype was also statistically different.

Table 18. Least squares means for liver weight (kg) by gene breed type

Gene breed type	n	*GHRL*	n	*LEP*	n	*NPY*
AA	58	$4.88 \pm 0.10^{a,b}$	45	5.08 ± 0.11^{a}	53	5.04 ± 0.10^{a}
AN	56	4.68 ± 0.10^{a}	47	$4.85 \pm 0.10^{a,b}$	49	4.70 ± 0.10^{b}
NA	54	5.04 ± 0.10^{b}	66	4.97 ± 0.09^{a}	64	4.99 ± 0.09^{a}
NN	55	$4.91 \pm 0.10^{a,b}$	56	4.71 ± 0.10^{b}	60	$4.78 \pm 0.10^{a,b}$

Least squares means with differing superscripts differ ($P < 0.05$)

Table 19 displays the least squares means for viscera weights due to gene breed type when contemporary group was included in the model. The AN gene breed type for *GHRL* had the lowest viscera weight. This reflects the same trend observed for liver weights where AN was the lightest gene breed type and fell outside the homozygote range. It is unclear why receiving a copy of the Angus *GHRL* gene from the sire and a copy of the Nellore *GHRL* gene from the dam could lead to smaller organ mass. The mid parent value for viscera weight was 64.68 kg, and the heterozygote average was 62.17 kg, which did not differ statistically ($P = 0.104$). The alternate heterozygotes differed ($P = 0.006$) and the breed of origin for the paternal haplotype approached significance ($P = 0.063$). As with liver weight, this difference seems to be entirely due to the difference between heterozygotes.

Table 19. Least squares means for viscera weight (kg) by gene breed type

Gene breed type	n	*GHRL*
AA	58	64.70 ± 1.29^{a}
AN	56	59.87 ± 1.31^{b}
NA	54	64.47 ± 1.37^{a}
NN	55	65.02 ± 1.32^{a}

Least squares means with differing superscripts differ ($P < 0.05$).

Table 20 exhibits the least squares means for ribeye area across gene breed type when contemporary group was included in the model. Animals that had AA gene breed type for the *LEP* gene had statistically larger ribeye than animals that had AN or NN gene breed types. However, animals with NA gene breed type were not statistically different from AA, AN, or NN gene breed types. For *LEP*, the mid parent value (72.39 cm^2) and heterozygote average (72.03 cm^2) do not differ statistically. The alternate heterozygotes and the contrast for breed of origin for the paternal haplotype were not statistically significant.

Table 20. Least squares means for ribeye area (cm^2) by gene breed type

Gene breed type	n	*LEP*
AA	45	74.00 ± 0.95^{a}
AN	47	71.29 ± 0.95^{b}
NA	66	$72.77 \pm 0.80^{a,b}$
NN	56	70.77 ± 0.86^{b}

Least squares means with differing superscripts differ ($P < 0.05$).

The least squares means for hot carcass weight due to the significant gene breed types are reported in Table 21. In regard to gene breed types for both *LEP* and *NPY*,

having 2 copies from Angus produced heavier carcass weights than having 2 copies from Nellore. However, the heterozygotes did not have statistically increased carcass weights as compared to the homozygotes. For *LEP* the mid parent value (297.94 kg) and heterozygote average (295.69 kg) did not differ. The mid-parent value for *NPY* (297.16 kg) and heterozygote average (294.13 kg) did not differ for carcass weight either. For the *LEP* gene breed type, the alternate heterozygotes did not differ significantly but the breed of origin for the maternal haplotype was statistically significant. For the *NPY* gene breed type, the breed of origin for the maternal haplotype was significant ($P = 0.017$) but the alternate heterozygotes did not differ ($P = 0.555$). It must be noted that for *LEP* and *NPY*, that the breed of origin for the maternal haplotype is confounded with the difference in the alternative homozygotes. A completely additive model would appear to give a good fit to the data.

Table 21. Least squares means for hot carcass weight (kg) by gene breed type

Gene breed type	n	*LEP*	n	*NPY*
AA	45	307.58 ± 5.05^{a}	53	306.12 ± 4.63^{a}
AN	47	$295.35 \pm 5.00^{a,b}$	49	292.23 ± 4.87^{b}
NA	66	$296.03 \pm 4.30^{a,b}$	64	$296.03 \pm 4.30^{a,b}$
NN	56	288.30 ± 4.59^{b}	60	288.20 ± 4.38^{b}

Least squares means with differing superscripts differ ($P < 0.05$)

In considering these traits, it has been assumed that there is a single allele of each in Nellore and a different allele in Angus, similar to what is assumed in a line-cross model for QTL analysis. However, examination of the SNP haplotypes for the region encompassing each gene suggests there may be multiple alleles of these 4 genes in each

breed. For *GHRL* haplotypes of 19 SNP there were 14 different Angus haplotyes observed in the F_1 parents and 8 different Nellore haplotypes in the F_1 parents. No haplotypes were shared across the 1 Mb region for *GHRL* between Angus and Nellore. For *LEP* haplotypes of 14 SNP there were 7 different Angus haplotypes observed in the F_1 parents and 3 different Nellore haplotypes in the F_1 parents, plus one of the *LEP* haplotypes was observed in haplotypes of both Angus and Nellore origin. For *IGF1* haplotypes of 12 SNP there were 8 different Angus haplotypes observed in the F_1 parents and 3 different Nellore haplotypes in the F_1 parents and none were shared across the 1 Mb region between Angus and Nellore. For *NPY* haplotypes of 6 SNP there were 7 different Angus haplotypes observed in the F_1 parents and 4 different Nellore haplotypes, plus one of the *NPY* haplotypes was observed in haplotypes of both Angus and Nellore origin. Effects of each haplotype will need to be evaluated in future work. Another explanation for the differences between alternate heterozygotes as well as the differences between breed of origin maternal and/or paternal haplotypes could be attributed to non-Mendelian inheritance patterns such as imprinting or other epigenetic factors.

4.2b Correlations among MPRC, Organ Weights, and Carcass Traits

Summary statistics are provided for MPRC, organ weights and carcass traits in Table 22 for the 232 Cycle I steers.

Table 22. Summary statistics for carcass traits and organ weights for 232 steers

Trait	n	Mean	SD	Minimum	Maximum
MPRC (kg/d)	232	0.00	1.37	-3.93	3.53
Fat thickness (cm)	232	1.21	0.45	0.25	2.43
Ribeye area (cm^2)	232	72.3	6.77	54.83	93.53
Hot carcass weight (kg)	232	296.95	35.44	189.23	389.09
Adj. fat thickness (cm)	232	1.4	0.46	0.38	2.54
Marbling right[1]	224	400.2	81.06	310	670
Marbling left[1]	227	400.37	79.12	310	650
Yield grade	232	3.307	0.55	1.9	4.8
Spleen weight (kg)	231	0.73	0.12	0.5	1.23
Viscera weight (kg)	229	64	10	36.95	101.45
Liver weight (kg)	231	4.89	0.74	3.18	7.68
Heart weight (kg)	207	1.54	0.24	1.02	2.24

[1] 400 = Small00. The right carcass side was electrically stimulated; the left side was not stimulated.

Correlations were calculated between MPRC, organ weights, and carcass traits among the 232 steers born from spring 2003 to spring 2007 are provided in Table 23 and 24 on pages 53 and 54. Robinson and Oddy (2004) reported genotypic correlations between RFI and rump fat (r = 0.72) and rib fat (r = 0.48) in analyses that included temperate and tropically adapted cattle and accounted for age and carcass weight; phenotypic correlations were 0.11 between RFI and rump fat and 0.13 between RFI and rib fat. Mader et al. (2009) reported a correlation between RFI and viscera weight of 0.18. A reason why no correlations were found between MPRC and any organ weight or carcass trait in this study, yet correlations were found between RFI and several of these traits in other studies, might be due to the method of calculation for MPRC as opposed RFI, but may also be due to differences in breed types across studies. A reported benefit

of using MPRC to evaluate feed efficiency is that MPRC should be used to evaluate animals across different contemporary groups. This is not possible with RFI as the calculation of RFI (average forced to be zero for each group) makes the values specific to each group of animals. Both MPRC and RFI are deviations from predicted intake relative to gain and weight. Mader et al. (2009) reported a statistically significant correlation (r = 0.34) between trim and kidney fat and RFI. In the 232 steers in this study, the correlation between MPRC and KPH was not statistically significant. The correlation between heart weight and RFI (r = -0.24), as reported by Mader et al. (2009), approached statistical significance (P = 0.06). In the 232 steer data set, MPRC and heart weight did not have a correlation that was statistically significant. The correlations between MPRC and viscera weight, liver weight, marbling, fat thickness, REA, KPH, HCW, and YG were not statistically significant, and Mader et al. (2009) also reported non-significant correlations of RFI with for these other traits. Mader et al. (2009) also examined the relationship between RFI and total fat (r = 0.15; P = 0.26) and lean (r = -0.10; P = 0.44), and those results seem to agree with the findings of this study when considering MPRC. Model predicted residual consumption was not significantly correlated to any measure of fat in this study, other than KPH. This could mean that cattle can be efficient in feed intake and still have the ability to obtain quality grades specific to a producers' needs.

Basarab et al. (2003) studied crossbred steers from various genetic background, but the majority of the breeds were *Bos taurus* with no significant relationship being

found between RFI and carcass marbling, *longissimus thoracis* area, and back fat thickness; this also appears to agree with the results of this study.

All of the organ weights had significant correlation with hot carcass weight, except for spleen weight. This might be due to the relationships of the functions of these organs to body function; for instance, the spleen is important for blood filtering and immune response and may be less related to total body size. In humans, Garby et al. (1993) studied 1,598 Danish adults who were healthy or who appeared to be healthy prior to death (1,086 males and 512 females). They reported a correlation between heart weight and liver weight of r = 0.45 for males and r = 0.38 for females, which are lower than the correlation reported in this study with cattle. Correlations between heart and spleen were also calculated for males and females (r = 0.29 and r = 0.30, respectively). In the current study, a correlation of r = 0.08 between spleen weight and heart weight was found. Garby et al. (1993) also calculated a correlation between spleen weights and liver weights for males (r = 0.39) and females (r = 0.36). No other reports among these organ weights have been found in livestock species.

Kidney, pelvic and heart fat is a common measure of internal fat on beef carcasses. A slight correlation between heart weight and KPH was reported in this study (r = 0.25; $P = 0.0002$). Rabkin (2006) stated that epicardial fat accounted for 20% of total heart weight in humans, so it is reasonable that heart weight in cattle could have been influenced by the amount of KPH fat on the carcass.

Organ weights in an adult Caucasoid population were collected from 684 cadavers. The organ weights of the cadavers (355 adult males and 329 adult females)

were collected from 1987 to 1991. The authors analyzed the relationship between organ weights and age, gender, height, and body mass index (BMI). The study reports linear interpolation results between heart weight and BMI and liver weight and BMI for males and females (males: $R^2 = 0.77$; $R^2 = 0.61$; females: $R^2 = 0.61$; $R^2 = 0.57$) (Grandmaison et al., 2001). These findings suggest that as the size of the heart and lung increases the cadavers overall size increases. These results are similar to the results found in this study.

Womack (1983) studied the relationship between fat deposits, body weight, and heart weight in 204 cadavers (43 female, 161 male) that ranged in age from 18 to 95 years, with a mean age of 66.4 years. There were 185 Caucasian cadavers and the remainder of the population was African-American. In men, Womack (1983) reported a correlation between epicardial fat weight and total body weight and total heart weight ($r = 0.42$, $P \leq 0.01$; $r = 0.37$, $P \leq 0.01$, respectively). For women, the correlation between epicardial fat weight and total body weight and total heart weight were both 0.49. It should be noted that the amount of cases to calculate the correlation between epicardial fat weight and total body weight was 14 and the correlation between epicardial fat weight and total heart weight used 18 cases. In the current study, statistically significant correlations between heart weight and hot carcass weight ($r = 0.58$) and between KPH and HCW ($r = 0.30$; $P = 0.0001$) were found. The results from Womack (1983) with humans were similar to the findings of this study with cattle. These findings suggest that larger hearts and higher amounts of fat surrounding the heart could be indicative of higher body weights.

Below are the correlations between the carcass data of the 232 steers in Table 23.

Table 23. Correlations between carcass data of 232 animal data set

	MARBL	FT	ADJFAT	REA	KPH	HCW	YG
MARBR	0.88	0.27	0.25	0.01	0.19	0.11	0.25
	<0.01	<0.01	<0.01	0.83	<0.01	0.10	<0.01
MARBL		0.26	0.24	0.04	0.19	0.13	0.25
		<0.01	<0.01	0.52	<0.01	0.05	<0.01
FT			0.94	0.20	0.23	0.50	0.84
			<0.01	<0.01	<0.01	<0.01	<0.01
ADJFAT				0.20	0.26	0.50	0.87
				<0.01	<0.01	<0.01	<0.01
REA					0.10	0.60	-0.09
					0.12	<0.01	0.16
KPH						0.30	0.46
						<0.01	<0.01
HCW							0.55
							<0.01

[1]Top value is r, and bottom value is *P*-value. MARBL and MARBR denote the amount of marbling in the left and right side of the carcass. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness; ADJFT= adjusted fat thickness; HCW = hot carcass weight; KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area

Table 24. Correlations among MPRC, organ data and carcass data of 232 steers

	MPRC	Liver	Heart	Viscera	MARBR	MARBL	FT	ADJFT	REA	KPH	HCW	YG
Spleen	0.02	0.00	0.08	-0.01	-0.10	-0.04	-0.06	-0.05	0	-0.04	-0.01	-0.06
	0.75	0.99	0.25	0.77	0.13	0.47	0.32	0.44	0.95	0.51	0.83	0.35
MPRC		-0.07	-0.01	-0.03	0.08	-0.04	-0.06	-0.08	0.06	-0.10	0.00	-0.10
		0.25	0.87	0.60	0.22	0.47	0.31	0.22	0.41	0.13	0.94	0.12
Liver			0.63	0.53	0.08	0.08	0.38	0.42	0.43	0.29	0.70	0.43
			<0.01	<0.01	0.21	0.21	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Heart				0.30	0.00	-0.01	0.15	0.13	0.25	0.25	0.58	0.58
				<0.01	0.94	0.84	0.02	0.05	<0.01	<0.01	0.0001	0.0001
Viscera					0.00	0.02	0.30	0.32	0.34	0.18	0.55	0.32
					0.97	0.80	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

[1]Top value is r, and bottom value is *P*-value. MARBL and MARBR denote the amount of marbling in the left and right side of the carcass. The right side was electrically stimulated; the left side was not stimulated. FT= fat thickness; ADJFT= adjusted fat thickness; HCW = hot carcass weight; KPH = kidney pelvic heart fat; YG = USDA yield grade; REA= ribeye area

5. SUMMARY AND CONCLUSIONS

The goal of this project was to; (1) investigate gene breed types for *IGF1*, *LEP*, *NPY*, and *GHRL* for their influence on feed efficiency (MPRC), visceral organ weights and carcass traits, (2) investigate the gene expression of *IGF1* in liver samples from animals previously identified to be divergent in feed efficiency (MPRC residual values) and investigate potential relationships of gene expression with visceral organ weight and carcass traits, and (3) evaluate correlations of MPRC, organ weights and carcass traits in F_2 *Bos indicus-Bos taurus* steers produced in Cycle I of the McGregor Genomics Project.

Sire and *IGFI* gene breed type nested within sire contributed to differences in *IGFI* RQ data in the 54 steers of divergent MPRC groups. Efficiency group accounted for differences in *IGFI* RQ data ($P = 0.05$). The average group had the highest amount of *IGFI* followed by the inefficient group and efficient groups, which were not different. Least squares means for *IGFI* RQ in the average, inefficient, and efficient groups were 1.46, 0.88, and 0.60, respectively. By sire, the mean range for *IGFI* RQ was 0.56 to 1.46. Additionally, *IGFI* RQ had a correlation approaching significance with liver weight ($r = -0.23$; $P = 0.09$).

Gene breed type was assigned for each candidate gene for each individual animal, and effects of these gene breed types were evaluated in single factor analyses for organ weights and carcass traits in both the 54-animal and the entire 232 steers. In the 54-animal data set, *GHRL* gene breed type influenced fat thickness ($P = 0.10$) and KPH

fat (P = 0.01); *NPY* gene breed type influenced fat thickness (P = 0.06), adjusted fat thickness (P = 0.03), and yield grade (P = 0.07), but neither *IGF1* gene breed type nor *LEP* gene breed type affected any other carcass trait, and, no gene breed types affected MPRC or visceral organ weights. Among all 232 steers, the *GHRL* gene breed type influenced liver (P = 0.08) and viscera weight (P = 0.01), *IGF1* gene breed type influenced fat and adjusted fat thickness (P = 0.04) and yield grade, *NPY* gene breed type influenced liver weight (P = 0.05) and hot carcass weight (P = 0.07), and *LEP* gene breed type influenced ribeye area (P = 0.03) and hot carcass weight (P = 0.01). Because substantial differences in many traits existed across contemporary groups, further analyses were conducted that included gene breed type along with contemporary group in the models. For these analyses where gene breed type was significant, least squares means were evaluated. Structured contrasts were generated to determine if the mid-parent value was significantly different from the heterozygote average, if alternate heterozygotes differed from each other, and if paternal or maternal line of descent effects existed. For liver weights, *GHRL* and *NPY* alternate heterozygotes were statistically different. Alternate heterozygotes were also different (P = 0.0062) for the *GHRL* gene breed type for viscera weight. Maternal origin of the haplotype was statistically significant for the *GHRL* gene breed type for liver weight and the *LEPT* and *NPY* gene breed types for liver weight and hot carcass weight. Paternal origin of the haplotype for the *GHRL* gene breed type for viscera weight approached significance and was not significant for the *LEP* gene breed type for ribeye area. In considering the contrasts for

maternal and paternal origin, the differences observed were due almost entirely to difference in the heterozygotes.

These results indicate that for these candidate genes evaluated in F_2 *Bos indicus-Bos taurus* crossbreds, there may be many phenotypic differences between *Bos indicus* and *Bos taurus* gene breed types (NN vs. AA) and there are also differences between alternate heterozygotes or maternal/paternal line of descent that should be considered and may indicate non-Mendelian inheritance patterns for certain genes in similar cattle populations. Further studies should evaluate other genes and other traits for a more complete understanding of how *Bos indicus* and *Bos taurus* cattle differ genetically and how crossbreeding these two types of cattle will impact morphological traits, feeding efficiency, and carcass traits.

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